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# Metabolism and thermoregulation in root voles (*Microtus oeconomus*) from the Qinghai-Tibet Plateau

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## Abstract

Metabolic rate and the role of evaporative water loss in thermoregulation were studied in root voles (*Microtus oeconomus*) from the Qinghai-Tibet Plateau. The thermoneutral zone is 28–32.5 °C. Mean basal metabolic rate is 3.29 ml $O_2$ $g^{-1}$ $h^{-1}$, higher than predicted values based on body mass. Total thermal conductance is 0.279 ml $O_2$ $g^{-1}$ $h^{-1}$ $°C^{-1}$, slightly higher than predicted values based on body mass. Evaporative water loss plays an important role in temperature regulation. All these characteristics have important adaptive significance for root voles to cope with their extreme environments. Cold and high altitude are the important factors to affect both metabolism and insulation. From an evolutionary point of view, long-time cold is perhaps the main selective force faced by root voles in their environment of the Qinghai-Tibet Plateau.

Key words: *Microtus oeconomus*, metabolism, thermoregulation

## Introduction

Many studies have concerned the ecophysiology of microtine rodent species and found that high metabolic rates are significant characteristics for these animals (Wunder 1985). However, only little information is available for species living at high altitude. Thus, we chose root voles (*Microtus oeconomus*) which have a very wide geographical range, and inhabit vast areas of the northern parts of the Euro-Asiatic continent (Gebczynska 1970), for physiological investigations. Root voles live in the *Potentilla fruticosa* shrub of alpine meadows on the Qinghai-Tibet Plateau. They are herbivorous, burrowing, winter active, and facing the two extreme environmental factors of cold and hypoxia. Therefore, the aim of this study was to investigate and characterize metabolic parameters of this species.

## Material and methods

### Animals

Animals were live-trapped at the Haibei Alpine Meadow Ecosystem Research Station of the Chinese Academy of Sciences, in the Menyuan County, Qinghai Province (37°29′ – 37°45′N, 101°12′–101°33′E). The altitude is about 3 200–3 500 m above sea level. The temperature range between day and night is great (minimum –2.6 °C to maximum 23.7 °C in July and from –35.2 °C to 6.1 °C in January). Comparing summer with winter, the differ-

ences of mean ambient temperature, mean maximum temperature, and mean minimum temperature were 21.9 °C, 17.8 °C, and 24.6 °C, respectively, during the years from 1980 to 1990. The plant growing period is short, only about 130–140 days. Average annual precipitation is 580 mm and mean wind speed is 3.1 m s$^{-1}$. Most snowfall occurs from September to June. The principal vegetation types are alpine shrub and alpine meadow. *M. oeconomus* were trapped in *Potentilla fruticosa* shrub in October 1992. The experiments were carried out in November 1992. Eight individuals (four males and four females) were used, of which the body mass was 24.0 g ± 1.0 (SE).

## Metabolic investigations

Metabolic rates were measured by using open flow respirometry with a Beckman OM-14 oxygen analyzer. Animals were tested in 0.5 l plastic chambers, equipped with air inlet and outlet ports. Metabolism chambers were kept in a temperature-controlled small room, and dry air from flow meters (Made by Shanghai Instrumental Co.) entered the chambers at 400 ml min$^{-1}$. Air flowed through columns of soda lime and drierite for removal of $CO_2$ and $H_2O$ before entering the oxygen analyzer.

Resting metabolic rate (RMR) was measured over the temperature range from 15 °C to 37.5 °C, as the lowest oxygen consumption sustained for 5 min of a quiescent, unanesthetized animal during 90 min in the respirometer. Measurements were carried out during daytime in darkened chambers. For reasons of stabilizing and becoming familiar with the chambers, the animals were in the metabolism chambers for 60 min, before oxygen consumption was recorded.

Metabolic rates were computed according to the method of DEPOCAS and HART (1957) and HILL (1972). The equation was as follows:

$$MR = \frac{F(F_{I_{O_2}} - F_{E_{O_2}})}{M(1 - F_{E_{O_2}})}$$

where MR is metabolic rate in ml $O_2$ g$^{-1}$ h$^{-1}$; F is flow rate at standard temperature and pressure conditions in ml min$^{-1}$; $F_{I_{O_2}}$ is the fractional oxygen concentration of inlet air; $F_{E_{O_2}}$ is the fractional oxygen concentration in outlet air; and M is body mass in g.

Each measurement lasted for 60 to 90 min. The animals were not fed 4 hours before the investigation in order to minimize the specific dynamic action of food.

## Evaporative water loss

When metabolic rate reached low readings, "U" shaped tubes packed with pre-weighed dry silica gel (to ± 0.1 mg) were connected to the outlet ports of the chamber for a further 30 min. The increase in weight of the U-tube over this time was taken as the evaporative loss (EWL) rate (DEAVERS and HUDSON 1981). The data of animals that urinated during the experiments were discarded.

All results were expressed as mean ± SEM, and regression analysis was used to analyze the relationship of energetic parameters with $T_a$.

## Results

### Oxygen consumption below the thermal neutral zone (TNZ)

Oxygen consumption increased with decreasing $T_a$ below the TNZ (Fig. 1); the relationship between resting metabolic rates (RMR) and $T_a$ (from 15 °C to 28 °C) is described by the equation:

RMR (ml $O_2$ g$^{-1}$ h$^{-1}$) = 9.011–0.200 $T_a$ (r = –0.986, p < 0.01)

The slope of the equation between RMR and $T_a$ was regarded as the total thermal conductance and it is proportional to heat loss from the body by radiation, conductance, convection, and evaporation. For the root vole this is 0.20 ml $O_2$ g$^{-1}$ h$^{-1}$ °C$^{-1}$. Using the
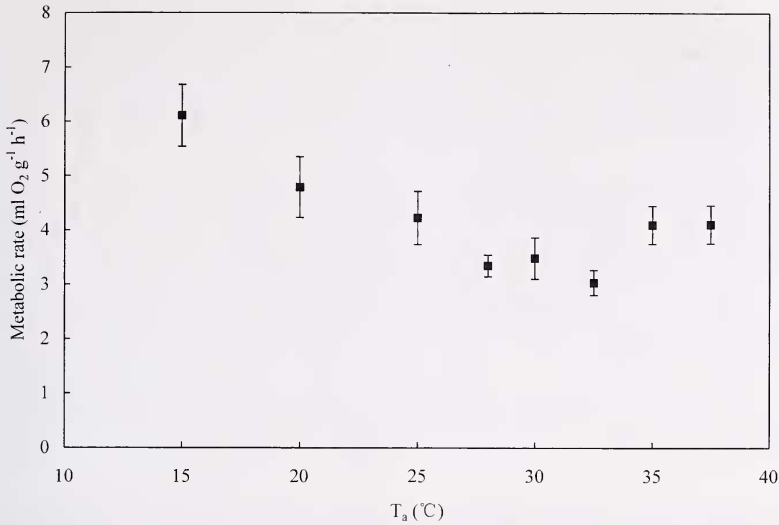
**Fig. 1.** Relationship of metabolic rates (ml $O_2$ $g^{-1}$ $h^{-1}$) to ambient temperature (Ta) in root voles. Bars indicate ± 1 SEM.

Newtonian model of cooling to calculate thermal conductance involves two assumptions. First, oxygen consumption should be linearly related to $T_a$; second, at RMR = 0, the intercept point of RMR and $T_a$ is equal to $T_b$. In the present study, the intercept of RMR and $T_a$ is 45.1 at RMR = 0, and this is much higher than the actual $T_b$ (38.5 °C) of root voles. McNab (1980 b) suggested that when the extrapolated $T_b$ is larger than the actual $T_b$ it should be corrected by the following equation:

$$C_m = C_f (1 + 0.06 \, \Delta T_b)$$

where $C_m$ is the minimum thermal conductance, $C_f$ is the slope of the regression equation between RMR and $T_a$, and $\Delta T_b$ is the difference between predicted $T_b$ at RMR = 0 and measured $T_b$. From this equation, $C_m$ is calculated to be 0.279 ml $O_2$ $g^{-1}$ $h^{-1}$ $°C^{-1}$, which is 37% higher than the value predicted by Herreid and Kessel (1967, $C = 1.0 \, W^{-0.50}$) and 42% higher than that predicted by Bradley and Deavers (1980, $C = 0.76 \, W^{-0.426}$).

## Oxygen consumption within and above the TNZ

The TNZ was 28 °C–32.5 °C. Within the TNZ, BMR was 3.29 ml $O_2$ $g^{-1}$ $h^{-1}$, 214% and 189% of the values predicted by Kleiber (1961, BMR = 3.42 $M^{-0.25}$, where M is the body mass in g) and Hayssen and Lacy (1985, BMR = 4.98 $M^{-0.33}$, where M is the body mass in g), respectively. Above the TNZ, RMR increased with $T_a$ (Fig. 1).

## Evaporative water loss (EWL)

EWL was relatively stable below the TNZ, with an average value of 5.48 mg $H_2O$ $g^{-1}$ $h^{-1}$. Within and above the TNZ, EWL increased with $T_a$, and reached a peak of 13.8 mg $H_2O$ $g^{-1}$ $h^{-1}$ at 35 °C. Above 35 °C, EWL declined and the root voles did not survive for more than 1 h (Fig. 2) There was a positive relationship between EWL and $T_a$ from 28 °C to 37.5 °C; this was described by the equation:

$$EWL \; (mg \; H_2O \; g^{-1} \; h^{-1}) = -13.54 + 0.74 \, T_a \; (r = 0.86, \, p < 0.05).$$
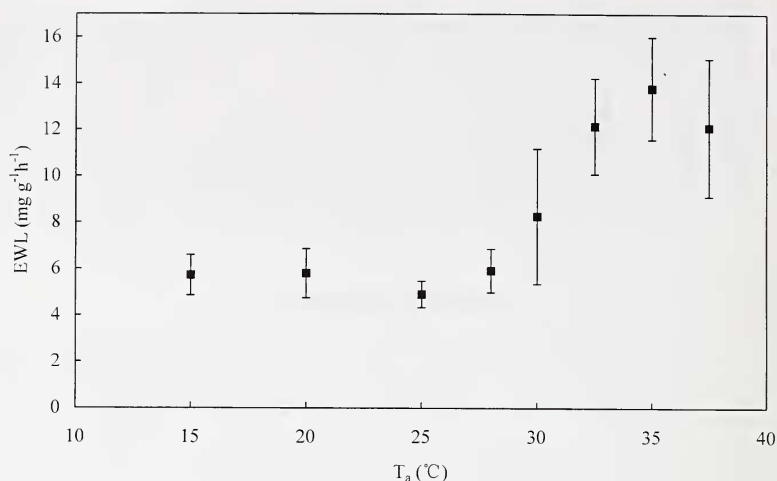
**Fig. 2.** Relationship of evaporative water loss (EWL, mg g$^{-1}$ h$^{-1}$) to ambient temperature (Ta) in root voles. Bars indicate ± 1 SEM.

Similarly, within the temperatures of 28 °C–37.5 °C, the ratio EWL/RMR was increased with increasing $T_a$; the regression equation is:

$$\text{EWL/RMR (mg } H_2O \text{ ml}^{-1} O_2) = -1.297 + 0.126 \, T_a \, (r = 0.85, \, p < 0.01).$$

## Discussion

This study shows that root voles living on the Qinghai-Tibet Plateau had higher values of metabolic rates (214% predicted by KLEIBER 1961). Similar results were reported for this species by JIA and SUN (1986, 221% predicted) and CASEY et al. (1979, 220% predicted). It seems that the high level of metabolism is characteristics for this species, regardless of whether they are distributed in taiga or on the Qinghai-Tibet Plateau.

Microtine species are generally distributed in boreal high latitude regions, where a high metabolic level is advantageous as an adaptation to the cold. Hypoxia, besides cold, in alpine regions is another important environmental factor. HAYS (1989) showed that at high altitudes deer mice (*Peromyscus maniculatus*) have a BMR that is higher than at low altitudes.

BMR may be modified by many factors, such as body size, food habits, activity, climate, and phylogeny (McNAB 1986, 1988, 1992) in mammals. For microtine species, their high metabolic rates are thought to be related to cold environments (PACKARD 1968), poorly digestible food (WUNDER 1985; KOTEJA and WEINER 1993), and intrinsic growth rate of a population (McNAB 1980a). McNAB (1992) also suggested that Arvicolids are characterized by a high basal rate of metabolism by general mammalian standards; and Arvicolids that live in cold climates, i. e., at high altitudes and latitudes, have higher basal rates of metabolism than species living in other environments. In alpine meadows, the annual mean temperature is –2 °C, and the mean maximum temperature in summer is only 15.6 °C (WANG and WANG 1996). Root voles here are exposed to cold environments throughout the year. Thus, a high BMR is beneficial to their survival at these high altitudes.

Generally, the thermal conductance of microtine species is lower than predicted va-

lues (Wunder 1985). Our study indicated that thermal conductance for root voles is 42% higher than values predicted from body mass (Bradley and Deavers 1980), which provides an effective avenue for heat loss. Slight high thermal conductance could be advantageous for this diurnally active species during the daily high temperature period. Mean maximum temperature of ground-surface may reach 34.9 °C in summer (Wang and Wang 1996).

EWL is very important for thermoregulation in root voles, even at high temperatures. Below the TNZ, the ratio of EWL to metabolic rate remained stable. Within and above the TNZ, the ratio increased sharply with Ta increasing and peaking at 32.5 °C, and then declining. This indicated that within the TNZ increasing rate of evaporative heat loss (EHL) was greater than that of metabolic heat production (HP), so the percentage of EHL to HP increased sharply with increase in $T_a$. Above the TNZ, the increasing rate of HP was greater than that of EHL, and the percentage of EHL to HP declined. This suggested that root voles have limited ability to cope with high temperatures.

If the EWL in root voles is expressed as the percentage of metabolic heat loss, it is 13% between 15 °C and 25 °C and 33% from 28 °C to 32.5 °C and 39% above. Bradley (cited by Deavers and Hudson 1980) found in seven species of voles that evaporative heat loss was 12% of total heat loss.

In summary, root voles from the Qinghai-Tibet Plateau had higher metabolic rates and slightly higher thermal conductance than predicted. Evaporative water loss plays an important role in thermoregulation, especially at high temperatures. A long period of cold and high altitude, a great temperature fluctuation between day and night, and a relative small temperature fluctuation within a year are perhaps important environmental factors to affect both metabolism and insulation for root voles.

## Acknowledgements

## Zusammenfassung

### Stoffwechsel und Temperaturregulation bei Nordischen Wühlmäusen (Microtus oeconomus) vom Qinghai-Tibet Plateau

Stoffwechsel und evaporative Wasserabgabe bei Thermoregulation wurden bei Nordischen Wühlmäusen (*Microtus oeconomus*) vom Qinghai-Tibet Plateau untersucht. Die Thermoneutralzone liegt bei 28–32,5 °C, und der mittlere basale Sauerstoffverbrauch ist mit 3,29 ml $O_2$ $g^{-1}$ $h^{-1}$ höher als auf der Grundlage des Körpergewichts erwartet. Der gesamte konduktive Wärmeverlust war ebenfalls höher als auf der Basis der Körpermasse zu erwarten war. Der evaporative Wasserverlust spielt eine wichtige Rolle bei der Temperaturregulation. Alle diese Charakteristika haben eine wichtige adaptive Bedeutung für Nordische Wühlmäuse in ihrem Habitat. Aus Sicht evolutiver Adaptation ist sehr wahrscheinlich die lang andauernde Kälte ein Hauptfaktor selektiver Einnischung.

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